

## Opinion

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# Notes on the evolution of unpalatability in butterflies by means of individual selection

In the following note, arguments are presented which challenge: 1) the evolution of unpalatability in butterflies by means of individual selection, 2) the hypothesis suggesting that Batesian mimics would have a good opportunity to evolve unpalatability by individual selection, and 3) an existing hypothesis for a mechanism of transition from Batesian mimicry to Müllerian mimicry.

R. A. Fisher (1930) recognized that natural selection acting on individuals was a plausible force leading to evolution of distastefulness. The arguments for the evolution of unpalatability by means of individual selection are essentially as follows: An individual carrying a mutation that renders it less palatable, and results in it being rejected more often by predators, will have a selective advantage over normal individuals similarly attacked if the more distasteful insect is able to escape and reproduce more often than the "normals" (Benson 1971; Harvey & Paxton 1981). The fundamental prerequisite for evolution of unpalatability in butterflies, by means of individual selection, requires that the distasteful mutant of a palatable species must survive the attacks of predators and subsequently reproduce.

Because there is no visual difference between the distasteful mutant and the normal palatable form, the only way for a bird (the main vertebrate predator of butterflies) to perceive that the mutant is distasteful is by tasting it. To survive, the mutant must be rejected by the predator and released unharmed after being caught, tasted and found distasteful. To be efficient and effective at this task, the specific chemical compound(s) that render the mutant unpalatable cannot be a toxin. This is because of the manifestation of the symptoms of toxicity are not instantaneous. For example, a bird vomits after consumption of a monarch (*Danaus plexippus* L.) containing at least one ED<sub>50</sub> cardiac glycosides or several monarchs with low toxicity containing a total of one ED<sub>50</sub> of the glycosides (Brower & Fink 1885). To be eaten, the monarch

must obviously be acceptable by the predator as palatable regardless of any toxin it contains. Logically, the chemical factor causing unpalatability must possess a flavor that the bird predator is able to taste, and on the basis of this taste, is then able to reject the prey promptly without harming it.

To taste a butterfly and release it unharmed (without disrupting the integument), the factor(s) rendering the butterfly distasteful (unpalatable) must be located on the water-impermeable outer surface of the wing or outer surface of the chitinous body and must be water-soluble. Only water-soluble substances in form of free molecules can be tasted (Zweers 1982). The outer surface of the chitinous integument and the wings, however, does not contain, nor it can retain, water-soluble molecules (see Kassarov 1999).

The only way a bird could taste a butterfly and release it unharmed requires tasting without disrupting the integrity of the integument. This may happen only with the minimal loss of a small part of the wing caught in the beak - beak-mark tasting, or by non-lethal pecking. Such precision is beyond the ability of a bird's gustatory apparatus. The apparatus is simply not sensitive enough in terms of the very small number of taste receptors (taste buds) and the manner of their distribution on the tongue and in the beak cavity. The issue is discussed in detail in Kassarov (1999, 2001)

By deduction the unpalatable mutant individual gains no protection from predator attack because there is no way for the birds to differentiate visually between the normal form and the new noxious mutant. To achieve protection, it is essential that the noxious mutant advertises its distasteful quality, i.e., it must acquire an aposematic color pattern as the theory of aposematism postulates. Thus, to avoid being attacked, the mutant must differ from the palatable normal form not only by taste. There must be a visible difference that the bird is able to discriminate and perceive as a warning signal that

the mutant individual should be avoided. However, the last condition further necessitates previous encounter(s) of the bird predator with the mutant, memorizing the encounter, recognizing the mutant and then differentiating it from the normal form. The mutant has to survive the encounter(s) to become fixed as a new form.

Thus, it seems reasonable that development of an aposematic (advertising) color pattern necessitates a simultaneous mutation in the color pattern of the mutant. However, novel warning variants gain no protective advantage from their color pattern, since predators cannot have previously encountered and learned their color patterns. This leads to frequency-dependent disadvantage of a rare variant within a species (Mallet & Singer 1987). Also, warningly colored variants may be more conspicuous than non-aposematic prey. "At very low frequencies, a conspicuous mutant will not be remembered however memorable it is because predators nearly always encounter it only once" (Mallet & Singer 1987). And "So little information is retained about conspicuous mutants by predators that their conspicuousness is a constant detriment because it increases the rate at which they are detected" (Servedio 2000). To perceive the new conspicuous color form (the mutant) as conspicuous, the bird has to taste it without disrupting the integrity of the integument and release it without diminishing its future reproductive success. The whole story gets entangled in a vicious circle.

Another factor widely considered responsible for the survival of aposematic butterflies (insects) is toughness and resilience of the integument. Wiklund and Järvi (1982) suggested that because many aposematic species are tough and difficult to kill (Cott 1940; Edmunds 1974), toughness would reduce the risk of lethal attack and allow enough distasteful individuals to escape to favor distastefulness. But "this begs the question of how toughness evolves" (Endler 1991). Thus, toughness of the integument cannot be considered as protecting the distasteful mutant of a palatable butterfly because the evolution of toughness must precede the mutation, or both must appear simultaneously or be genetically linked. There are no published data concerning a causal relationship between toughness of the integument and chemical compounds that may render the insect distasteful. Such a relationship could exist if based on a chemical reaction as, for

example, polymerization, that provides a hardened chitinous integument. It seems highly improbable that chemical compounds that supposedly render a butterfly distasteful simultaneously cause the integument to become tough and resilient.

Thus, a survival of the mutant must be stochastic: the mutant simply was not caught by a predator and managed to mate and reproduce by chance. Random predation, given a very low initial frequency, may confer relative protection of the rare mutant that might thus increase its chance for survival. The mutant may subsequently increase in frequency, but this will occur only as long as the frequency of the mutant remains very low (see Mallet & Singer 1987, Endler 1991).

While the unpalatable mutant remains very rare, it will be effectively "hidden". So, what selective forces could lead to an increase in frequency of the mutant? There is no apostatic selection because the bird predator cannot exert a selective pressure. In order to exert selective pressure, the bird must be able to recognize both the unpalatable mutant and the palatable form and avoid the mutant. Since there is no visual difference between the distasteful mutant and the palatable form, the frequencies of mutants and palatable normals in the population will not be subjected to selection, and the rare mutants will receive no advantage.

Huheey (1961) stated that "it seems likely that unpalatable characteristics are often eliminated from populations when in the incipient stages simply because the bearers did not survive the tasting procedure and the characteristic was not as yet sufficiently widespread to benefit the entire population;" and further suggested, "that Batesian mimics would have a good opportunity to evolve unpalatability by individual selection. Being protected from attack by the model, any tendency to develop distasteful qualities will be enhanced since predators would attack and taste them cautiously." Under this scenario, it is the palatable mimic that mutates to unpalatability. Since both mimic and distasteful mutant are protected by the model, and because there is no visual difference between the mimic and the mutant, both would be attacked with equal caution. The bird perceives them as the same variety in the same manner as a distasteful mutant of a palatable butterfly not mimicking a distasteful one. Since the mutant is, in fact, a mimic of the model, but unpalatable (distasteful), and the bird perceives it as

a mimic, this will lead to an increase of the frequency of the distasteful form in the population. As a result, there will be a new distasteful form that is phenotypically unrecognizable from the mimic and with a color pattern more or less resembling the model (depending on how advanced is the progression of the Batesian mimicry). The more perfect the mimic, the more closely the mutant will resemble the model. Accordingly, the community will maintain both the distasteful Batesian model and the distasteful mutant differing from the model not only by strength of distastefulness but also by the substance(s) determining the distastefulness.

Huheey (1961) also advanced a mechanism for the transition from Batesian to Müllerian mimicry. The problem with this mechanism is that again, not only is the distasteful mutant protected by the model, but the palatable Batesian mimic is protected as well. The model equally protects both. However, because there is no visual difference between the Batesian mimic and the mutant, the mutant is not protected by apostatic selection and bird predation cannot be a selective factor for the stabilization of the mutant.

Evolution of Müllerian mimicry via Batesian mimicry predicts that the palatable Batesian mimic should be selectively eliminated from the population by predation: i.e. it must lose protection by the model. The mutant, however, should remain fully protected by the model and continue to reproduce. Accordingly, the community will maintain both the distasteful Batesian model and the distasteful mutant. I cannot perceive a mechanism by which the bird predator can both selectively eliminate the mimic and selectively protect the rare mutant. Thus I consider the hypothesis suggested by Huheey (1961) questionable. On the basis of the arguments presented, I question the proposed mechanism for the development of unpalatability in palatable butterflies based on individual selection.

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